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HOW EXPERIMENTAL PHYSIOLOGY AND ECOLOGICAL NICHE MODELLING CAN INFORM THE MANAGEMENT OF MARINE BIOINVASIONS?

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ABSTRACT

Marine bioinvasions are increasing worldwide by a number of factors related to the anthroposphere, such as higher ship traffic, climate change and biotic communities' alterations. Generating information about species with high invasive potential is necessary to inform management decisions aiming to prevent their arrival and spread. *Grateloupia turuturu*, one of the most harmful invasive macroalgae, is capable of damaging ecosystem functions and services, and causing biodiversity loss. Here we developed an ecological niche model using occurrence and environmental data to infer the potential global distribution of *G. turuturu*. In addition, ecophysiological experiments were performed with *G. turuturu* populations from different climatic regions to test predictions regarding invasion risk. Our model results show high suitability in temperate and warm temperate regions around the world, with special highlight to some areas where this species still doesn't occur. Thalli representing a potential temperate region origin, were held at 10, 13, 16, 20 and 24ºC, and measurements of optimal quantum field (Fv/Fm) demonstrated a decrease of photosynthetic yield in the higher temperature. Thalli from the population already established in warm temperate South Atlantic were held at 18, 24 and 30°C with high and low nutrient conditions. This material exposed to the higher temperature demonstrated a drop in photosynthetic yield and significant reduction of growth rate. The congregation of modelling and physiological approach corroborate the invasive potential of *G. turuturu* and indicate higher invasion risk in temperate zones. Further discussions regarding management initiatives must be fostered to mitigate anthropogenic transport and eventually promote eradication initiatives in source areas, with special focus in the South America. We propose that this combined approach can be used to assess the potential distribution and establishment of other marine invasive species.

Keywords: *Grateloupia turuturu*, invasive marine algae, populational ecology, ecophysiology, anthropogenic impacts.

1. INTRODUCTION

Marine bioinvasions are receiving great attention as many of them are producing negative socio-environmental-economic impacts worldwide (Katsanevakis et al., 2014). Offshore oil exploitation, aquaculture activities and ballast water are major vectors responsible for growing events of non-indigenous species arrival and spread (Creed et al., 2017; Hulme, 2009). Climate change further facilitates the dispersal of marine organism by increasing the frequency and intensity of extreme climatic/oceanographic events (Sissini et al., 2017, 2014; Ummenhofer and Meehl, 2017). A diverse and abundant array of vectors for the transport of organisms across biogeographic boundaries coincides with disrupted native communities of marine organisms, caused by both global (ocean acidification and warming) and local stressors (coastal pollution, overfishing) (Shea, 2002), which is facilitating the establishment of non-indigenous species on coastlines all around the world (Occhipinti-Ambrogi 2007). Williams and Smith (2007) estimated that there are 277 introduced seaweed species around the globe, with the Mediterranean and the North-East Atlantic being the most highly invaded regions. The geographical distribution of marine macroalgae is determined by their physiological tolerance to environmental conditions (Breeman, 1988; Hoek, 1982), enabling the prediction of suitable habitats for invasive species (Elith et al., 2006; Marcelino and Verbruggen, 2015). Ecological Niche Models (ENM) relate occurrence data with environmental gradients to produce habitat suitability maps (Peterson, 2003). An ability to assess the risk of invasion and the threats posed by foreign organisms helps managers and stakeholders put preventive measures in place and optimize biosecurity monitoring (Marcelino

and Verbruggen, 2015). Eradication of established populations is costly and usually ineffective (Bax et al., 2001; D'Antonio and Meyerson, 2002). The known occurrence of species informs predictive distribution models, which can be misleading since this depends on sampling effort and identification expertise which varies widely depending on the species and regions investigated (Verbruggen et al., 2009). ENM do not consider the physiological traits of species when modelling distributions, likely missing valuable information about the mechanisms and processes allowing the presence and establishment of populations (Marcelino and Verbruggen, 2015). Therefore, physiological information can be used to validate and further improve ENMs to create a more accurate prediction of habitat suitability (Martínez et al., 2015).

Considering species traits related with dispersal, establishment and ecological impact, the fifth most dangerous invasive alga in a global perspective is *Grateloupia turuturu* Yamada (1941) (Nyberg and Wallentinus, 2005), commonly known as the "Devil's tongue weed" (Mulas and Bertocci, 2016). *G. turuturu* can displace native species in rocky intertidal habitats (Freitas et al., 2016; Mulas and Bertocci, 2016), has advantage establishing in recently perturbed environments, where native assemblages are disrupted (Mulas and Bertocci, 2016), and has been reported for reducing the abundance and richness of invertebrates (Janiak and Whitlatch, 2012; Jones and Thornber, 2010). Native to Japan, *G. turuturu* has been documented as an invasive species in the United States (Balcom and Yarish, 1994; Mathieson et al., 2008), Mexico (Aguilar-Rosas et al., 2012), New Zealand (D'Archino et al., 2007), France (Simon et al., 2001), Italy (Cecere et al., 2011), Portugal (Araújo et al., 2011), Australia (Saunders and Withall, 2006), and Israel (Tsiamis et al., 2015). This species was recently registered for the coast of South Brazil, being the first record of this species in the South Atlantic (Azevedo et al., 2015). The transport of oyster for aquaculture and ballast water are the main probable vectors of *G. turuturu* introduction in the

Atlantic and Mediterranean (Araújo et al., 2011; Harlin and Villalard-Bohnsack, 2001). Important dispersion vectors may also be yacht and ship hulls, as specimens have been found attached to such boats in France (Simon et al., 2001). *G. turuturu* has been described to tolerate a wide range of temperature (from 4 to 28ºC), salinity (from 15 to 37), nutrients (Simon et al., 2001) and can be found down to a depth of 7m (Sweet 2011). Liu and Pang (2010) described lower photosynthetic activity in *G. turuturu* when exposed to freezing, which further explains why this species is mostly found, until now, in temperate regions. However, even with the description of *G. turuturu* being tolerant to a great spectrum of environmental conditions in the North Atlantic and Pacific, there is no descriptions of the South Atlantic population tolerance to the local oceanographic conditions, nor experiments that describe the biochemical processes of its ecophysiological performance. For this reason, ecophysiological experiments are necessary to better understand the influence of temperature and nutrients in *G. turuturu* physiology and assess its probability of success in regions with conditions similar to the native range.

In this study we developed an ENM to estimate the global potential distribution of *G. turuturu.* In addition, we determined the ecophysiological thresholds of *G. turuturu* as a tool to infer about the species resilience and temperature tolerance. Our hypothesis is that *G. turuturu* will present higher habitat suitability and physiological performance in temperate regions. By combining ENMs and the physiological thresholds evaluation, we desire to propose this associated approach to foster coastal management strategies related not only to *G. turuturu* bioinvasion, but also to invasions by other marine species.

2. MATERIALS AND METHODS

2.1 Ecological Niche Modelling

To develop the ENM for *G. turuturu*, six environmental benthic data layers (i.e., along the bottom of the ocean) were extracted from Bio-ORACLE (Assis et al., 2017b; Tyberghein et al., 2012) based on the biological relevance of macroalga (Assis et al., 2017a, 2014; Neiva et al., 2015) (environmental predictors used in the model are described in Table 1). Depth was not included as a predictor as it has no direct biological meaningfulness in the ecophysiological response of macroalgae, and many previous works modelling marine macroalgae also do not include it (Jueterbock et al., 2016, 2013; Tyberghein et al., 2012). Bio-ORACLE data has been widely used for marine ecological modelling (Marcelino and Verbruggen, 2015) since it contains climatic and geophysical data with a global spatial resolution of 0.08º (9.2 km). Detailed georeferenced occurrence data from both invaded and native ranges was obtained from the public Global Biodiversity Information Facility (GBIF, 2018), and literature data (available in the supplementary material ESM1) (e.g. Tyberghein et al. 2012; Escobar et al. 2016). The inclusion of the invaded range in the model increases model accuracy, as models trained using data only from the native range usually fail to predict the full invasion extent of a species (Beaumont et al., 2009; Broennimann and Guisan, 2008). Duplicated occurrences, outside marine range or too close to each other (5 km²) were excluded to prevent biases and reduce spatial autocorrelation in the analyses, remaining 106 records (Figure 1). The radius of 5 km² was chosen as an conservative distance of about half of the resolution of the climatic data used in the model, seeking spatial independence between the environmental data of occurrences (Phillips et al. 2009; Kramer-Schadt et al. 2013). The modelling approach combined multiple cross-validation interactions using independent datasets with Boosted Regression Trees (BRT), a statistical algorithm able to fit complex non-linear relationships between a response (occurrence records) and predictor variables (environmental data), while avoiding overfitting through optimized parameterization procedures

and specific forcing of monotonic responses (Elith, Leathwick, & Hastie, 2008). BRT algorithm is known for high predictive performance (De'ath, 2007; Neiva et al., 2014), improving its performance by combining many models for prediction, which makes it a more accurate algorithm when compared to other regression methods (Elith, Leathwick, & Hastie, 2008). In the lack of absence data, presence-only modelling requires the generation of pseudo-absences or background information (e.g., Maxent; Phillips et al. 2006). This information was produced using the method developed by Senay et al. (2013) for improved ecological modelling, which comprise the calculation of environmentally dissimilar regions to the presence points and the random selection of pseudo-absences in clustered climatic predictors to reduce the use of redundant information. To account for likely sources of sampling bias, pseudo-absences were chosen from a kernel probability surface developed with the records of occurrence over a grid with the same resolution of environmental data (e.g., Phillips et al. 2009; Assis et al. 2018a)

Cross-validation interactions were developed by partitioning species records (i.e., presences and also pseudo-absences) into 10 independent longitudinal bands to evaluate the performance of models (Wenger and Olden, 2012). Models fitted with one withheld band at a time, and True skill statistics (TSS) compared this data to the outcomes of a predicted surface of distribution reclassified to reflect presence and absences (binomial) with a threshold maximizing TSS. Over-fitting in the models was reduced by tuning the algorithm parameters (i.e., learning rate, number of trees and tree complexity; see Elith et al. 2008; Assis et al. 2016, 2018a for details) and also by forcing monotonic responses (positive for minimum nutrients, salinity, light and temperature; negative for maximum temperatures). Final predictions using optimal parameters were reclassified to binomial responses and its final accuracy was reported with AUC (Area Under the receiver operating characteristic Curve, Fielding and Bell 1997), sensitivity (true positive rate)

and TSS (True Skill Statistics, Allouche et al. 2006). The significance of models was determined by inferring the relative contribution of each environmental predictor to the performance of the models (Elith et al., 2008). Physiological limits points (maximum and minimum, depending on the predictor) were determined by extracting the individual fitting function of each predictor alone, while fixing the alternative predictors in their average (Elith et al., 2008; Marcelino and Verbruggen 2015).

ENM analyses were performed with R (R Development Core Team, 2017) using the packages dismo, gbm, parallel, raster, SDMTools, and sm.

2.2 Ecophysiological experiments

Two populations of *G. turuturu* were ecophysiologically evaluated considering different acclimatization histories. A warm temperate adapted population (WAP) was sampled (approximately 100 g of fresh weight (FW)) on August 22nd, 2016 from the intertidal zone of Itapirubá beach (28°20'14.32"S, 48°42'4.87"W), in the city of Imbituba, Santa Catarina, Southern Brazil. A temperate adapted population (TAP), approximately 60 g FW, was also sampled in Saint Malo beach (48°39'32.8"N 2°00'24.6"W), France, on February 20th, 2017, region representing a possible source of *G. turuturu* germlings through oyster seeds or ballast water. Since a determined biomass of *G. turuturu* was collected, which included individual blades and blades attached together by a holdfast, all samples were separated in individual blades. The sampled blades of both populations presented around 6 cm height and 2 cm in width, were not fertile, collected in winter, immediately transported in plastic containers with seawater to the lab, and manually cleaned from epiphytes or associated fauna after sampling.

To determine the control conditions for each of the experimental designs, we considered the different adaptation conditions of each population. Therefore, the temperate and warm temperate populations were exposed to conditions observed in their respective occurrence regions (~10ºC in France in February (Dubois et al., 2007), and ~18ºC in Imbituba in August (Gouvêa et al., 2017)). Both populations were cultivated in 250 mL Erlenmeyer flasks, in UV sterilized seawater enriched with Von Stosch medium in a 50% concentration, without EDTA chelating salt (adapted from Edwards 1972) until the beginning of the experiment. To prevent the lack of essential nutrients water was replaced daily. Aeration was provided individually in the flasks, also stirring the water in each flask to disrupt the diffusive boundary layer. The temperature was adjusted by heaters (Radical 1 HP, Brazil) positioned in trays with water, where the treatment flasks were kept in a water bath. Each tray contained one data logger (HOBO Pendant Temperature/Light Data Loggers, Onset, Bourne, USA) that recorded the water temperature every 10 minutes. A 12-hour light/dark photoperiod was used, and irradiance was provided by fluorescent lamps with an average of 65±5 μmol photons m^{-2} s^{-1}.

The experimental design performed in Brazil had as main purpose to observe short-term ecophysiological effects of temperature and nutrients, key environmental drivers selected according to conditions found in adjacent tropical environments where the species has not been reported yet (Gouvêa et al., 2017). The WAP sampled blades were brought to the laboratory, and acclimated for 21 days to laboratory irradiance, maintaining field temperature (18ºC). Initial and final 1g FW samples were frozen with liquid nitrogen for the analysis of biochemical descriptors. The experiment lasted for seven days. The experimental setup in Brazil utilized three temperatures (18, 24 and 30ºC) and two nutrient conditions: one without medium culture (Low Nutrient Concentration – LNC) and another with 50% of Von Stosch (VS) medium (High Nutrient

Concentration – HNC), resulting in 6 factorial treatments. Each treatment contained 10 replicas (*n* = 10), consisting of individual blades of *G. turuturu* weighted to sum 1g FW per Erlenmeyer flask.

The experiment performed with the temperate adapted population, a potential source of *G. turuturu*, has as main purpose the investigation of the short-term ecophysiological effects of temperature, an environmental driver traditionally related with the distribution constraints of marine algae (Hoek, 1982). The chosen temperature values used in the experiment are present in the region of the North Atlantic where the algae were sampled (Dubois et al., 2007), expect for the higher temperature used. The higher temperature used was chosen to overlap with conditions observed in the warm temperature region, providing the necessary scenario for the evaluation of the potential ecophysiological continuum, contribution to the discussion about invasive potential of *G. turuturu.* For the TAP experiment realized in France, *G. turuturu* blades were acclimated for three days at 10ºC, temperature observed in the water of the sampling location. *G. turuturu* was exposed for 60 hours to 5 different temperatures: 10 (control), 13, 16, 20 and 24ºC. Each treatment contained 6 replicas (*n* = 6), also consisting of individual blades of *G. turuturu* weighted to sum 1g FW. The experiment duration was limited by laboratory structure and the availability at Saint Malo. Figure S1 on the supplementary material ESM2 illustrates the different experimental designs of both populations.

2.3 Physiological analyses

Physiological analysis performed in both populations were measurements of optimal quantum field (Fv/Fm). Growth rate and photosynthetic pigments were only evaluated in the WAP experiment, as the biomass sent to Brazil lost minimum preservation conditions due to

transportation delay. Considering the relevance of Fv/Fm as a descriptor, we chose to keep the results obtained in the TAP experiment.

2.3.1 Photosynthetic yield

In the WAP experiment, effective quantum yield (Fv/Fm) was estimated by the fluorescence of *in vivo* chlorophyll *a*. Three measurements of Fv/Fm were made in each replica in different parts of the thallus, resulting in 3 subreplicas of each one of the 10 replicas. Measurements of Fv/Fm were taken with a pulse-amplitude modulated chlorophyll *a* fluorometer (Diving PAM – Walz Germany) after acclimation in the dark for 20 minutes in the first day, then every two days, and in the last day of the experiment (for further explanation of the methodology followed, see: de Ramos et al., 2018; Figueroa et al., 2006). For the TAP experiment, measurements of Fv/Fm were made in the dark only in the end of the 60 hours.

2.3.2 Pigment extraction

At the end of the experiment, all the replicates from the WAP experiment were frozen and used for pigments quantification. Each replica was divided in 3 portions of 100 mg, allowing the reading of 3 subreplicas, which resulted in 30 extractions for each treatment. The extraction followed Schubert et al. (2011), where phycobiliproteins, chlorophyll *a* and total carotenoids were extracted from the same 100 mg biomass sample grinded in liquid nitrogen. Phycobiliproteins were extracted first with phosphate buffer (pH 6.8) and kept in the dark at 4ºC for 2 hours until centrifugation for 4 minutes at 13000 rpm in the MiniSpin centrifuge (Eppendorf) at room temperature. Subsequently, the supernatant was used to determine the concentration of phycobiliproteins according to Beer and Eshel (1985). Afterwards, methanol 100% was placed on

the same biomass and kept in the dark at 4ºC overnight, and then centrifuged as stated before. Then, chlorophyll and total carotenoids were quantified according to Torres et al. (2014). Absorbance was determined in the SpectraMax Paradigm Multi-Mode Microplate Reader (Molecular Devices), of the Laboratório Multiusuário de Estudos em Biologia (LAMEB).

2.3.3 Growth rate (GR)

To determine the daily growth rate (GR), replicates were spun for 15 seconds in a salad spinner to reduce the excess of water, and then weighted in an analytical balance. The replicates were weighted in the first and last days to determine the GR by the following equation (Lignell and Pedersén, 1989):

$$\mathrm{GR}\ (\%.\,\mathrm{day}^{-1}) = \left[\left(\frac{Wt}{Wi}\right)^{1/t}\right] \times 100\% \qquad (1)$$

Where Wi and Wt are respectively the initial and final fresh weight after *t* days (t = 7 days).

2.4 Statistical analysis

For the WAP experiment, the independent variables considered were time (beginning and end), nutrient concentration (HNC and LNC) and temperature (18, 24 and 30ºC). For Fv/Fm, time was considered for the 1st, 3rd, 5th and 7th day. For significant differences, post-hoc test of Tukey was used to identify significantly different groups ($p<0.05$). The TAP experiment had as variables only the different temperatures, 10, 13, 16, 20 and 24ºC, with 6 replicates ($n=6$).

Each treatment of the WAP experiment had 10 replicates ($n=10$), which were used for the analysis of GR. However, in the reading of pigments and Fv/Fm, some of the replicas presented negative values or values too close to zero, representing errors in the readings. This required the removal of 3 replicas in each treatment (resulting in a $n=7$), to maintain the same number of

replicates for statistical analysis. Before analysis, data were tested for normality and residuals for half-normality. Statsoft Statistica 13.0 was used to perform multifactorial Analysis of Variance (ANOVA, $p<0.05$). Due to the removal of outliers, the data did not require transformation, as it attained the normality requirements for the ANOVA parametric tests calculated.

3. RESULTS

3.1 Ecological Niche Modelling

The final predictive model had high performance (AUC: 0.96; Sensitivity: 0.95; TSS: 0.93) and showed that *G. turuturu* has great habitat suitability in temperate regions of Northern Pacific, Northern Atlantic, South America, Australasia (Oceania) and a small portion of Southern Africa (Fig. 2). Light at bottom and maximum ocean temperature were the most important predictors to the ecological niche of *G. turuturu*, while nutrients (as nitrates and phosphates) were the least important (Table 1). Response curves showed habitat suitability with light above 4.4 E . m^{-2} . yr^{-1} and ocean temperature bellow 26.55ºC, however, with a starting drop at 21.23ºC (Fig. 3). Response curves of the other variables used in the model are available in the supplementary material ESM2 (Figures S2, S3, S4, S5 and S6).

3.2 Ecophysiological experiments and physiological analyses

3.2.1 Photosynthetic yield

In the WAP experiment, there was significant interaction ($p<0.05$) between temperature, time and nutrient concentration for Fv/Fm (Table 2). A decline in Fv/Fm was noticeable as the temperature increases and through the experiment time in WAP (Fig. 4). The treatment of 30ºC with HCN showed the lowest values in the fifth and seventh day of treatment in comparison with

297 the treatments with lower temperatures. For 30ºC with LNC, there was a smaller decline in Fv/Fm,
298 but still presented Fv/Fm values lower than the treatments of 24 and 18ºC. Similarly, there was a
299 contrast between the LNC and HNC treatments at 24ºC, with lower values of Fv/Fm observed at
300 HNC. In France, statistical analysis of TAP experiment results of Fv/Fm showed significant
301 difference between temperatures (Table 2). The response of *G. turuturu* to the short-term exposure
302 in the TAP experiment to different temperatures was of lower Fv/Fm in the treatment of 24ºC (Fig.
303 5).
304
305 3.2.2 Photosynthetic pigments
306 No significant interaction (p>0.05) was found for both GR and pigments with time,
307 temperature, and nutrient concentration (i.e., no three-factorial interaction for GR and pigments).
308 However, regarding chlorophyll *a*, total carotenoids and GR, when the effects of nutrient
309 concentration are taken out, the interaction between time and temperature was significant (p<0.05).
310 For phycoerythrin and chlorophyll *a* the interaction between the effects of time and nutrient
311 concentrations was significant (Table 3). For chlorophyll, the treatments of 24ºC and 30ºC in the
312 end of the experiment were statistically distinct from the samples of the beginning and 18ºC (Fig.
313 6a). The higher concentration of chlorophyll was found in 30ºC, followed by 24ºC. Similarly, the
314 higher concentration of total carotenoids was found in the last day at 30ºC, and all the other
315 treatments had the same lower concentration (Fig. 6b). Additionally, for chlorophyll there was
316 statistical difference between different nutrient concentrations. On the end of the experiment, the
317 HNC treatment presented higher values of chlorophyll, as in LNC the concentration remained
318 close to the one in the beginning of the experiment (Fig. S7 on the supplementary material ESM2).
319 On the other hand, there was a decrease in phycoerythrin concentration in the last day in LNC,

while at the treatment of HNC remained constant throughout the experiment (Fig. 7). Concentration of phycocyanin was not detectable.

3.2.3 Growth rate

For daily growth rate, only temperature and time were significant (Table 3). The algae exposed to 30ºC showed lower GR when compared to the algae in lower temperatures (Figure 6c).

2.4 DISCUSSION

The investigation of the potential geographic distribution through ENM and physiological thresholds tested through experiments of *G. turuturu* indicated higher habitat suitability of this invasive species in temperate and warm-temperate regions around the world. Experimental results demonstrated a decrease in photosynthetic yield in algae exposed to higher temperatures, along with a stress response observed in pigments and growth rate. At the same time, ENM showed a possible expansion of the distribution of *G. turuturu* to new countries around the globe, especially in regions with temperatures close to the ones that the algae better adapted in the experiments.

The variables that most contributed to explain the distribution of *G. turuturu* were the availability of light at bottom and maximum ocean temperatures. Light at bottom is determined with an exponential decay function of photosynthetic active radiation, diffuse attenuation coefficient and depth (Assis et al., 2017b) and allows restricting the species vertical distribution. Indeed, the 4.04 E. m^{-2}. yr^{-1} threshold is comparable with the minimum annual irradiance inferred for other species of algae (Gattuso et al., 2006). The limitation of 26.55ºC maximum temperature inferred in ENM was also in line with previous descriptions of Simon et al. (2001) for the species occurrence in Brittany (France), where waters can reach up to 28ºC in summer. The relative

discrepancy in these values can arise from the short term variations of temperature in the water pools where Simon et al. (2001) described the occurrences, which are not captured in the averaged climatic layers used for modelling. In fact, our experiment results show, the warm temperate population of *G. turuturu* can maintain its photosynthetic yield for at least three days in this temperature, demonstrating that this alga can survive to short-time exposure to high temperatures.

In addition, the temperate population experiment demonstrated *G. turuturu* similar Fv/Fm responses to temperature as the response curve from the model, with higher photosynthetic yield in 10, 13, 16 and 20ºC. The experiment with the blades collected in Brazil also showed higher Fv/Fm in the lower temperature used. These results indicate that both populations of *G. turuturu* present better physiological performance in regions with mild temperatures, i.e. temperate climates. Interestingly, in higher temperatures the two populations responded differently. As stated above, the WAP population presented tolerance to a short-time exposure to 30ºC, and to 24ºC for the duration of the experiment (LNC only), while the TAP population had a significant drop in performance in 24ºC. Although the different responses may be relative to the fact that these are two distinct invasive populations (Allendorf and Lundquist, 2003), both demonstrated the tendency to experience a drop in Fv/Fm in higher temperatures. The higher temperature used in the warm temperate experiment demonstrated that *G. turuturu* will also present reduced growth rate in regions with average temperatures around 30ºC. Even with the higher chlorophyll content, *G. turuturu* was not able to maintain its photosynthetic yield in 30ºC. Furthermore, the higher concentration of total carotenoids showed a stress response of the algae to the higher temperature but did not prevent the reduction of growth. However, previous studies of the species demonstrated that younger stages of *G. turuturu*'s life cycle have a wider temperature tolerance range than older stages, with germiling growth being the same at 15ºC and 30ºC (Kraemer et al., 2017). For this

366 reason, juvenile stages and/or spores may be more aggressive in a bioinvasion process if
367 transported by an oceanographic vector. And once in a new habitat, the acclimation conditions
368 during the invasive process may be determinant in the success of establishment, when temperature
369 limits are between the ones here evaluated for adult blades.

370 The ecophysiological experiment in Brazil showed that *G. turuturu* can tolerate a wider
371 range of nutrient concentration without reducing its photosynthetic yield in 18ºC, which was
372 expected based on previous descriptions of this algae (Simon et al., 2001). The region where the
373 species is found in southern Brazil is characterized by the presence of upwelling of colder, nutrient-
374 rich waters from the South Atlantic Central Water, and during winter receives influence from the
375 nutrient-rich La Plata river plume and the cold waters of the Sub-Antartic currents (Pereira et al.,
376 2009). Simultaneously, Martins et al. (2012) reported the algae diversity decrease in southern
377 Brazil caused by urbanization and coastal pollution, damaging the resilience of the benthic
378 community. Consequently, the local conditions of this region meet the suitable conditions
379 demonstrated by the experiment and the model for the establishment and expansion of *G. turuturu*
380 occurrence. Hence, countries with similar coastal characteristics with no register of the species
381 must be aware and act to prevent the arrival and establishment of *G. turuturu.*

382 Our results allow the affirmation that non-fertile adult blades of *G. turuturu* will likely not
383 have success in expanding its niche to regions with an average temperature around 30ºC or survive
384 to heatwaves (short periods with an average of 5 days of anomalous warming of the ocean)
385 (Hobday et al., 2016) in regions with milder temperatures. As for temperate and warm-temperate
386 regions, our model predicts habitat suitability for *G. turuturu* for temperatures reaching up to
387 approx. 26ºC, and the WAP experiment results demonstrated that this alga can maintain its
388 photosynthetic yield and growth at 24 ºC. However, if in 24ºC an event of introduction of a higher

amount of nutrients in the water column occurs, *G. turuturu* may suffer a drop in photosynthetic yield depending on the exposure period. Consequently, the invasive potential of this alien species in regions with an average temperature around 24ºC may be smaller than its potential in colder water regions, as noted in the 18ºC treatment, where *G. turuturu* had no response to the higher nutrient concentration.

Temperature was chosen as one of the variables in the experiments and model due to its importance in determining the geographic distribution of macroalgae (Hoek, 1982). The changes in the average sea surface temperature caused by climate change are characterized as a global stressor to autochthonous communities. *G. turuturu*, as demonstrated in this study, can have advantage in such scenario, expanding its distribution to locations with predicted regional cooling (e.g. northern Chile and South Africa, Falvey and Garreaud 2009; Bolton and Anderson 2012) or warming of cold-water regions (Poloczanska et al., 2013; Vergés et al., 2014). Models as the one here used are the best approach to translating future climatic changes into ecological responses, guiding strategies of conservation and management (Wiens et al., 2009). Moreover, the effects of a local stressor, higher nutrient concentration, were assessed in *G. turuturu* through ecophysiology evaluation. By combining both approaches, we could determine the possible geographic expansion of *G. turuturu* under both local and global stressors.

Habitat models for invasive seaweeds need a high transferability, expanding predictions to regions where the species could potentially invade. Verbruggen et al. (2013) demonstrated that for global predictions the most important procedure to increase model transferability is choosing fewer predictors with high ecological significance for the species. Furthermore, the use of ecophysiological knowledge about the species is highly advisable to assess the significance of

predictions (Araújo and Guisan, 2006). Accordingly, we used ENM and fewer variables to model the global distribution of *G. turuturu* together with the evaluation of its ecophysiology.

With increasing environmental changes and availability of transport vectors, it is essential the use and improvement of approaches capable of predicting possible new events of bioinvasion, as done in this work. Invasive species represent great harm to ecosystem services, with provision services being the most affected by them, such as food provision and genetic variability (Vilà et al., 2010). It becomes clear that these predicting tools and the knowledge of invasive species and their habitats must be used as the foundation of international regulatory agreements, pursuing the protection of natural resources and biodiversity (Hulme et al., 2008). The results found in this study enable stakeholders and policymakers to discuss and foster management actions regarding prevention or eradication in case of *G. turuturu* expanding its distribution to new regions, especially for South America where there are few registers of its occurrence (Azevedo et al., 2015). Therefore, the present work takes place as an important tool of bioinvasions management in a scenario of quick changes in environmental conditions and dispersion patterns, in which the delay of response by international and local governments can cost the planet ecosystem functions and services that it relies upon.

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Figure captions

Fig. 1 Map of *G. turuturu* occurrences used in the model. Sampling locations are represented in white diamonds, whilst black dots represent occurrences in the known introduced range and grey dots represent occurrences in the native range. A close-up was made in South America to show more clearly the introduced and sampled locations in this region.

Fig. 2 Map of *G. turuturu* habitat suitability in the planet (a), with zoom in South America (b), and Europe/North Africa (c). Regions in black represent regions suitable for the occurrence of *G. turuturu,* whilst regions in light grey represent regions with unsuitable environmental conditions for *G. turuturu.* Land is represented in dark grey, and zones without environmental data are represented in white (no data).

Fig. 3 Response curve of *G. turuturu* to maximum ocean temperature. Decline point is set at 21.23^{o}C and the limiting point at 26.55^{o}C, demonstrating low habitat suitability of *G. turuturu* to higher temperatures.

731 **Fig. 4** Average ± standard deviation (*n*=7) of Optimal Quantum Yield (Fv/Fm) for all
732 temperatures (18, 24 and 30ºC) and nutrient conditions (low nutrient condition – LNC, and high
733 nutrient concentration – HNC) in the first, third, fifth and seventh day of the warm temperate
734 adapted population (WAP) experiment. Letters indicate Tukey's test significantly different
735 groups (p<0.05).

736 **Fig. 5** Average ± standard deviation (*n*=6) of Optimal Quantum Yield (Fv/Fm) in the temperate
737 adapted population (TAP) experiment in the beginning of the experiment (initial control), then
738 the values of each treatment after three days at 10 (control), 13, 16, 20 and 24ºC. Letters indicate
739 Tukey's test significantly different groups (p<0.05).

740 **Fig. 6** Response of *G. turuturu* (warm temperate adapted population - WAP) to different
741 temperatures in treatments. Different letters represent Tukey's test significantly (p<0.05)
742 different groups. Bars represent average ± standard deviation. (a) Chlorophyll *a* concentration
743 (µg chlorophyll-*a* per g of fresh weight) in the experiment's beginning and end (*n*=7). (b) Total
744 Carotenoids concentration (µg total carotenoids per g of fresh weight) in experiment's beginning
745 and end (*n*=7). (c) Percentage of *G. turuturu* daily growth rate during the experiment (*n*=10).

746 **Fig. 7** Average ± standard deviation (*n*=7) of phycoerythrin concentration (µg phycoerythrin per
747 g of fresh weight) at different nutrient conditions (warm temperate adapted population - WAP).
748 Letters indicate Tukey's test significantly different groups (p<0.05).

749

750 Supplementary material

751 **ESM1:** Excel file with all the occurrences and their sources used in the Ecological Niche Model.

752 **ESM2:** Word document with additional figures, such as the experimental design setup, response
753 curves of the model and chlorophyll concentration in each nutrient condition (WAP experiment).

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